

ON *CEPHALASPIS LYELLI* AGASSIZ

by ERROL WHITE

ABSTRACT. The type specimen of *Cephalaspis lyelli*, the genotype of *Cephalaspis*, has never been fully described nor properly figured, and its counterpart has hitherto been completely ignored. Both parts of the specimen have been further developed, especially the counterpart, and are here described in detail. The position of the species in Stensiö's proposed new classification is established on the form of the oralo-branchial chamber. No other specimen of this species is known.

INTRODUCTION

IT is a remarkable fact that *Cephalaspis lyelli* Agassiz, the type-species of *Cephalaspis* and therefore the basis of the whole group of the Osteotrachi or Cephalaspidomorphi, has never been properly defined nor the unique type-specimen adequately described. Until now this has not been of much consequence since cephalaspids are of characteristic form and easily recognized, while the genera comprising the group have been readily distinguishable on external characters. My friend Professor Stensiö has allowed me the privilege of reading parts of the proofs of his article for the *Traité de Paléontologie*, and in it he is proposing a classification in which the numerous species now referred to the genus *Cephalaspis* are divided among three genera in as many different Orders or Sub-orders. The basis of this remarkable proposal is the form of the mouth region and of the branchial pouches, features so seldom seen that the great majority of species (there are some ninety described) 'ne peuvent . . . être actuellement rattachées à un genre', while 'Le génotype de *Cephalaspis*, *C. lyelli* Agassiz, a une chambre oralobranchiale mal conservée et il est par suite peu probable qu'on puisse jamais définir et déterminer à quel orde il appartient'.

Stensiö's remarks regarding the condition of the oralo-branchial chamber of *C. lyelli* are not applicable. While it is true that at the moment there is only one specimen known of this species, there is no reason why others should not be found, and what he says of the unique lectotype is fortunately not now correct and, whether one accepts Stensiö's new classification or not, it is possible to determine the position of *Cephalaspis* in it, and to say which of his genera is its synonym.

HISTORY OF THE SPECIES

The genus *Cephalaspis* was described by Agassiz in 1835 (p. 135, pl. 1*a*, 1*b*) and to it were assigned four species, *C. lyelli*, *C. rostratus*, *C. lewisi*, and *C. lloydi*. The last two were removed by Kner in 1847 to form the types of a supposed cuttlefish *Pteraspis*, and in 1858 T. H. Huxley showed that they were the ventral plates of a species of 'fish' of which *Cephalaspis rostratus* was the dorsal armour, leaving *C. lyelli* as the only original species of *Cephalaspis*, and therefore the type species.

As was usual at that time Agassiz based his description of the species on an indeterminate number of specimens from Scotland and England of which he figured five (pl. 1*a*, figs. 1 and 2; pl. 1*b*, figs. 1, 3, 5). The last specimen, which looks like a piece of a pteraspid, is apparently lost, so that the other four figured specimens are the only ones now identifiable and are therefore the only effective co-types.

Forty-five years later Ray Lankester (1870, p. 43, &c.) redescribed these co-types, and removed three out of the four to other new species, the originals of Agassiz's pl. 1*a*, fig. 1 and pl. 1*b*, fig. 1 to *C. powriei*, and of pl. 1*b*, fig. 3 and all other English specimens to *C. agassizi*, leaving the specimen figured in pl. 1*a*, fig. 2 as the lectotype, by elimination, of *C. lyelli*. This famous specimen, which was given to the British Museum in 1846 by Sir Charles Lyell himself, was refigured by Lankester (pl. 8, fig. 1) in a much improved representation by Mr. Dinkel, the same artist who had drawn Agassiz's original figure thirty-five years before. In the meantime the specimen had undergone considerable change; much of the tail had been uncovered and so had the lower part of the body-scales especially of the right side, but in clearing the sides from the matrix, which is a hard coarse sandstone, most of the pectoral paddles had been destroyed. It is, however, from Agassiz's original figure that the representation of this specimen in Murchison's *Silurian System* (1839, pl. 1, fig. 2), in the various editions of *Siluria* (e.g. 5th edit., 1850, pl. 37, fig. 1) and in numerous textbooks to the present day, have been taken.

Lankester added another specimen, from Arbroath, to the species (1870, pl. 11, figs. 1, 2) but even in its imperfect state it seems too wide in the head, and to have too few rows of body-scales, to be conspecific. He also published a rather primitive restoration of the species (text-fig. 16, p. 41).

Woodward (1891, p. 179) reunited the English specimens described as *C. agassizi* with *C. lyelli*, but he did not figure the type-specimen (No. 20087), but contented himself with reproducing Lankester's restoration. Curiously enough he did not notice that a second, fragmentary specimen (P. 3233), which he described as 'Portions of head and trunk of similar specimen; Glamis', was in fact part of the counterpart of the lectotype. Somehow it had become separated from the major specimen and came to the Museum in the Earl of Enniskillen's great collection in 1882, thirty-six years after the other part.

Stensiö (1932, p. 119, text-fig. 40, pl. 15, fig. 1), in his distinguished work on the British Cephalaspids, gives a very restricted account of the species. He was unable to figure the lectotype as it was then not possible for the specimens to leave London, and the counterpart as then developed added little or nothing to the known details. He stated that 'The exoskeleton of the cephalic shield is much weathered and therefore not in a condition for detailed study'. In fact the specimen was not weathered at all, but when the counterpart was split off it left, for the most part, only the basal layer on the major specimen, while the details of the counterpart were obscured by the other bony layers. Stensiö tentatively placed in the species (1932, pl. 15, fig. 1) specimens from Brechin, which are now shown clearly to be unrelated. Possibly they belong to a form of *C. powriei*.

DESCRIPTION OF LECTOTYPE

The main portion (B.M. No. 20087), that described and figured by Agassiz and others, consists of an almost complete animal, virtually an internal cast. The cornua show only the bone of the underside. The paddles are now badly mutilated. The extreme tip of the snout is damaged and about half of the tail is missing, doubtless removed when the block of sandstone was originally trimmed, for the whole of the tail at this time was covered in matrix and its presence unsuspected. The specimen is not quite symmetrical, for the right side has been slightly crushed, as the dorso-lateral scales show, but the left side is almost undistorted.

The counterpart (B.M. No. P. 3233), now in the form of an external mould, comprises only part of the right side from the level of the front of the orbit to the spine of the (posterior) dorsal fin. The cast shows to some extent the condition of the original specimen in Agassiz's time, for the pectoral paddle is present, but only part of the cornu shows and none of the ventro-lateral scales or the tail. Fortunately the central area of the shield with the cephalic spine and the ridge scales and dorsal fin are well preserved.

The main specimen and counterpart will be described together.

As preserved the specimen measures 20.5 cm. in length. The complete animal measured about 24.5 cm., as can be judged by comparison with a specimen of *C. pagei* figured twice natural size by Stensiö (1932, pl. 35, fig. 3), for the two figures coincide closely in the length of the head-shield, and in the position of dorsal fin and the root of the tail.

The length of the cephalic shield to the tip of the brief spine is about 8.0 cm., almost exactly one-third of the animal's total length, and the maximum breadth, across the posterior part of the cornua, a little less, about 7.8 cm. The breadth narrows forwards and the front of the shield was almost certainly rounded. The distance of the front margin to the pectoral sinus is on average 6.7 cm., and to the tips of the cornua 9.5 cm., so that the cornua were about 2.8 cm. long. The interzonal part at its posterior end is 3.4 cm. broad, less than half the maximum breadth of the shield. The maximum height, at the base of the dorsal spine, is now 1.5 cm., but was probably nearly 2 cm. since the cornua, especially on the right side, are bent upwards. There are no denticles on the inner margin of the cornua but there seems to have been a small but distinct pectoral angle.

The interzonal part is short and to it is attached one undivided scale-row, while two others are incompletely separated from the base of the spine on each side. It bears a low but well-defined crest ending in a short, hooked, laterally compressed spine.

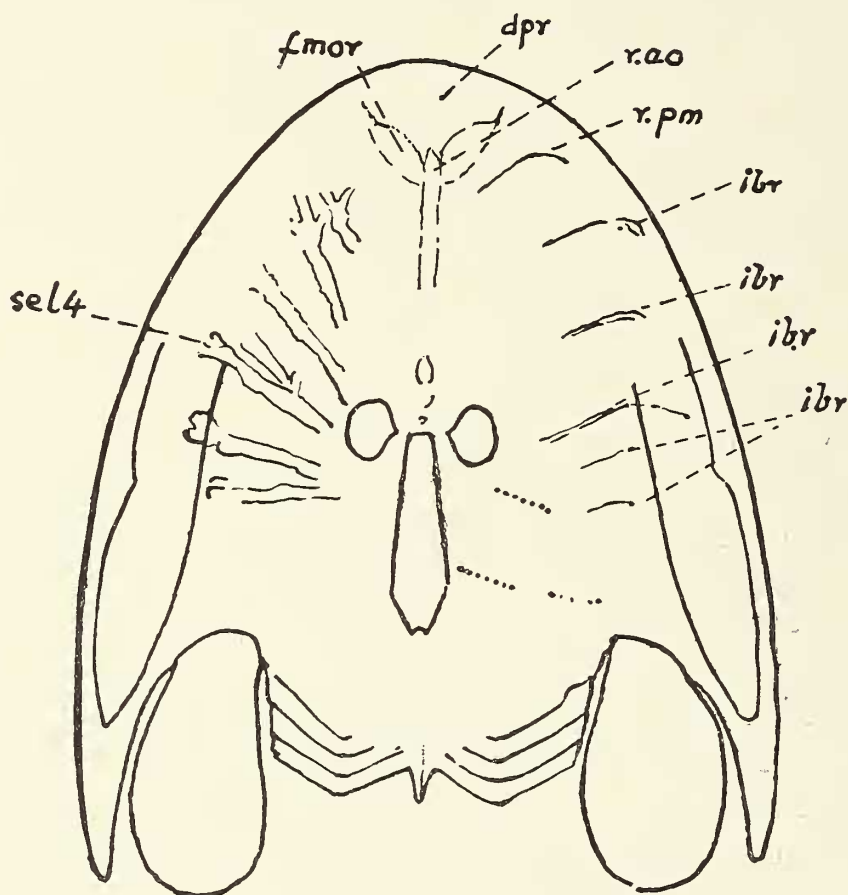
The orbits are oval, of moderate size, 0.65 cm. long and 0.45 cm. wide with an inner median projection. They lie at the middle of the length of the shield measured from the tip of the snout to that of the dorsal spine and are thus much nearer the pectoral sinuses than to the front margin. The position of the hypophyseal sac is clearly indicated in front of the orbits. The median dorsal sensory field is very well preserved in impression in the counterpart and is most distinctive in shape. It is very long and narrow. The length is 2.2 cm. with perfectly straight sides diverging gradually to the rear, the breadth being only 0.3 cm. at the front margin and increasing gradually to 0.7 cm. at a point 0.4 cm. from the hinder end. It then narrows rapidly to 0.2 cm. in front of the dorsal spine where it ends with a slight re-entrant angle. The hinder two-thirds of the right lateral field is similarly preserved. It runs well on to the cornu, for about 1 cm. and ends in a blunt point. The field is relatively broad, about 0.8 cm. at its maximum. The marked notch on the outer margin is very probably an individual defect.

As Stensiö (1932, p. 121) has noted, the endoskeleton is imperfect but at least some of the perichondrial bone-layers were present, such as the orbital and labyrinth layers and those which lined the canals of the lateral sensory fields; but on the whole the skull was very lightly ossified. A fair proportion of each of the six sensory canals can be seen on the left side, and, more obscurely, parts of the other vessels as well.

The supra-oral field (*dpr*), roughly triangular in form, is very faint, without a transverse ridge, and extends only a short distance to the aortic ridge (*r.ao*), and the paratoral depressions (*f.mor*) are likewise inconspicuous and virtually absent. Most important are

the clear indications of the pre-branchial (*r.pm*) and inter-branchial ridges which by their obliquity clearly indicate that the species falls within Stensiö's group Oligobranchiata, while the form of the oral area places it within his family Zenaspidae. *Cephalaspis* is identical with Stensiö's *Zenaspis*, as one might have expected by its general form.

The right pectoral limb is well preserved as an impression in the counterpart. It is paddle-shaped with a rounded contour, measuring 2.9 cm. in length and 1.7 cm. wide at



TEXT-FIG. 1. Head-shield and pectoral paddles of the lectotype. Slightly restored. $\times \frac{4}{5}$. *dpr*, supra-oral field; *f.mor*, paratoral field; *ibr*, inter-branchial ridges; *r.ao*, aortic ridge; *r.pm*, pre-branchial ridge.

the maximum. Faint indications of overlapping scales are shown, chiefly near the outer margin.

The cast of the counterpart shows that the superficial layer of the exoskeleton was continuous and the surface unornamented, the fine irregularities to be seen being due to the coarseness of the matrix. The mucous canal system was entirely enclosed in the exoskeleton. Only here and there are the tesserae of the sensory fields to be detected.

Indications of two pit-lines are visible, *cm* and *cmm*₁+*cmm*₂.

None of the exoskeleton of the oralo-branchial region on the undersurface is preserved.

The trunk is exposed except the undersurface (which indeed appears to be absent) and

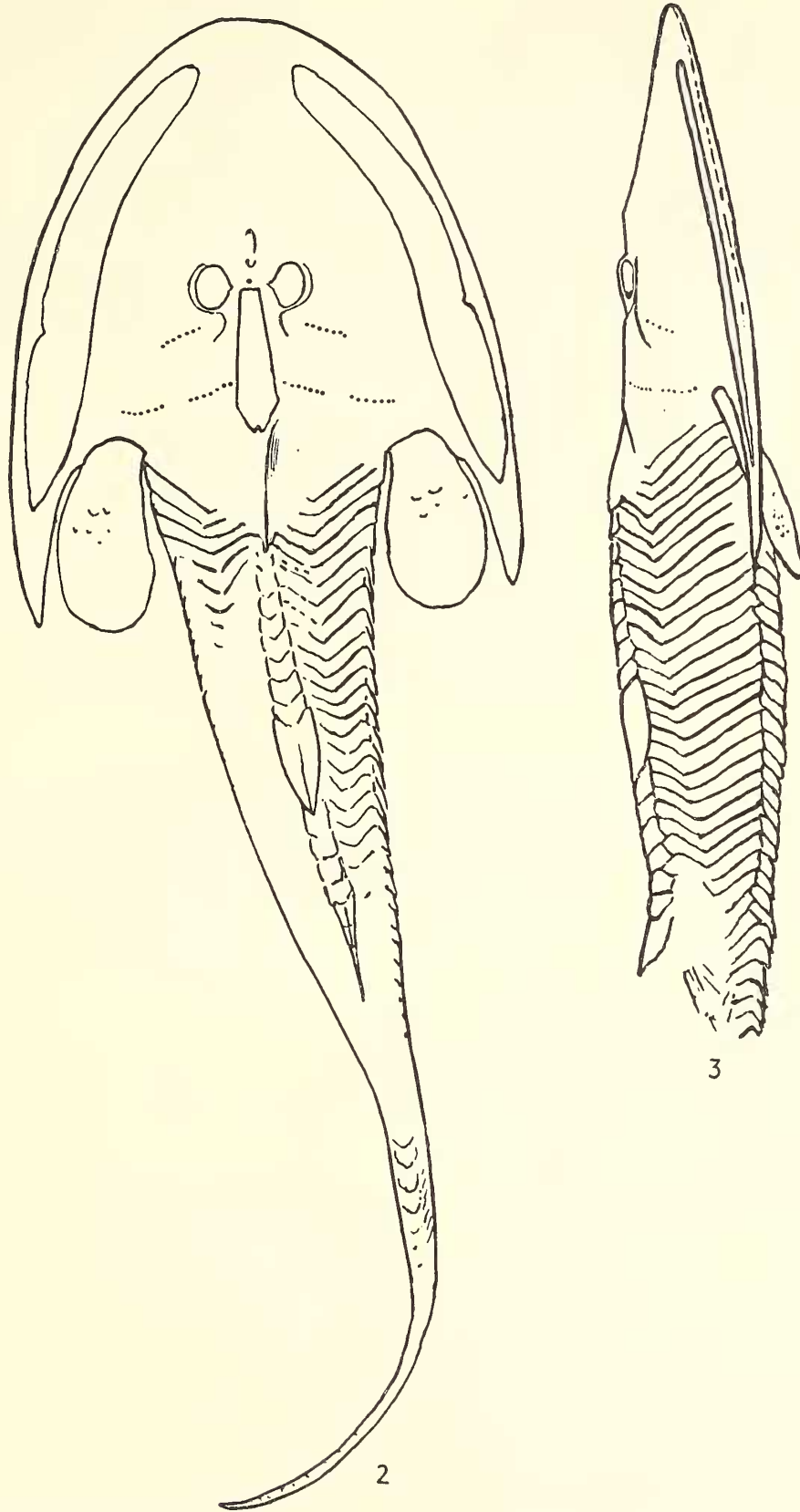
EXPLANATION OF PLATE 18

Figs. 1-2. *Cephalaspis lyelli* Agassiz. 1, The lectotype, dorsal view. The specimen is 20.5 cm. long. The ridge-scales are missing. Lower Old Red Sandstone, Glamis, Angus, Scotland. B.M. (N.H.) No. 20087. 2, The same specimen, side-view.



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the lower part of the left side, which is still covered in matrix. In form the body is triangular with well-rounded sides. It was about 3.0 cm. high and 3.5 cm. wide at the base in front, immediately behind the interzonal part. It decreases rather rapidly both in



TEXT-FIG. 2. *Cephalaspis lyelli*. Outline of complete animal. $\times \frac{2}{3}$.

TEXT-FIG. 3. *Cephalaspis lyelli*. Head and body, side view. $\times \frac{2}{3}$.

height and breadth towards the tail. The animal was therefore a good deal flatter than in *Hemicyclaspis* (cf. Stensiö 1932, text-fig. 15, p. 53), but the form of the squamation was essentially the same. There are, however, important differences, of which the more obvious

are that there are far fewer rows of scales with broader and shallow flank-scales, and that the flank-scales and dorso-lateral scales were fused together.

Including the three partially fused rows in front there are thirty-seven scale-rows to the root of the tail, as against some fifty-five in *Hemicyclaspis*. The fused dorso-lateral and lateral scales form a conspicuous angle with one another (somewhat exaggerated by crushing in Pl. 18, fig. 2) since the former slope backwards and the latter forwards, the angle in the middle of the body being about 90° , becoming slightly greater in front and increasingly more acute towards the tail. The scales of course overlap one another backwards, the breadth of the exposed surface of the larger scales being rather less than 0.3 cm. on the slightly concave right side and rather more on the convex left side. The breadth of the overlapped area is uncertain. The height along the scale of the dorso-lateral part is 1.1 cm. at about the ninth scale, that of the main lateral scales about twice as high. The main lateral part of the scales decreases rapidly at the level of the hinder end of the enlarged dorsal ridge-scale, that is from about the twentieth row, and at the level of the twenty-seventh under the dorsal fin, the dorso-lateral parts break up into a mosaic.

The azygous row of A-shaped ridge-scales again slopes backwards more or less parallel with the main lateral portions, forming a similar angle with the dorso-lateral parts, but they are much lower, being only 0.4 cm. in height. They do not correspond with the scale-rows, being broader, about 0.35 cm. There are nine from the sixth scale-row, that immediately behind the cephalic spine, to the sixteenth. From the seventeenth to the twenty-second rows there is a single large ridge-scale, representing the remains of the anterior dorsal fin, and then three rather long ridge-scales corresponding to scale-rows 23–27 immediately followed by the spine of the dorsal fin. The spine is deep and pointed, formed by three distinct pieces, much laterally compressed. No part of the fin itself is preserved but the series of ridge-scales behind it starts over scale-row 36 and gradually diminishing in size continues as far as the specimen is preserved.

The tail is very crushed, although much of it is now free from the matrix. The scales on the axis were very small and arranged obliquely upwards and backwards, much as in *Hemicyclaspis*.

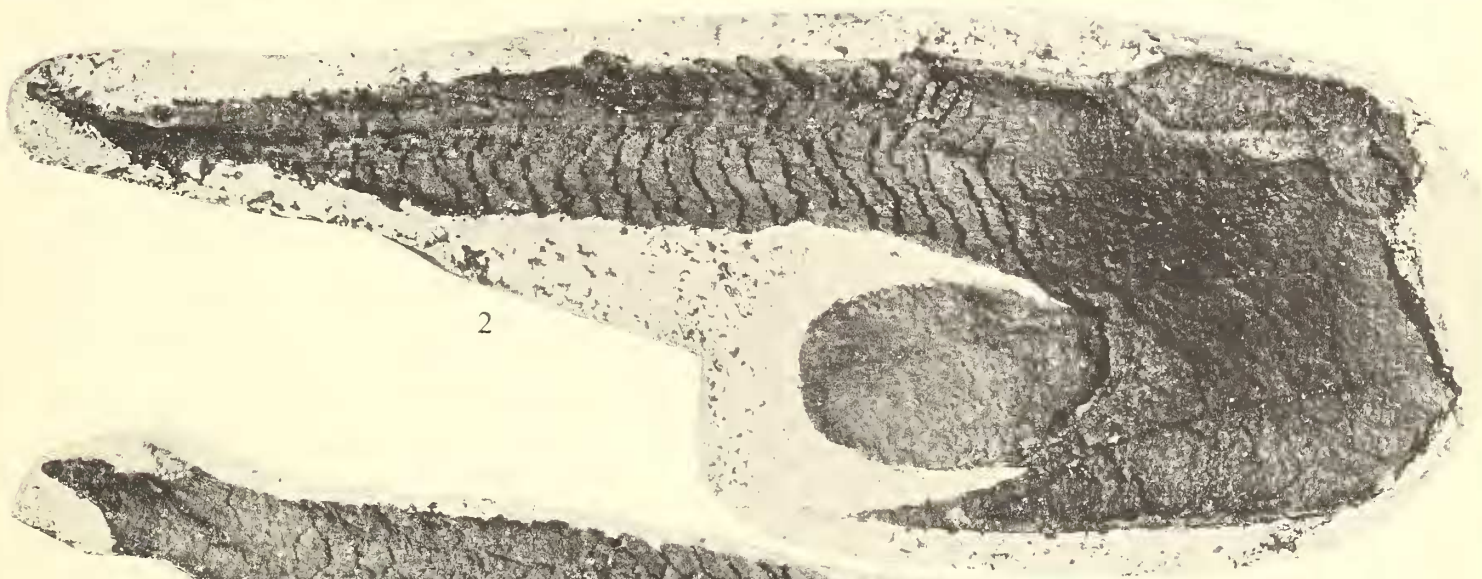
The ventro-lateral series of scales, exposed only on the right side, correspond with the scale-rows, but are separate from the lateral scales, with which they form the same sharp angle as the other series do with one another. The largest are 6.0 cm. in height and end in a free point directed ventro-laterally. They continue right to the base of the tail.

As noted above, none of the undersurface of the body is exposed, and it would appear, from trial excavations, that the ventral scales, which form most of the under surface, and those covering the oralo-branchial chamber, have been lost.

This species has several characteristic features that distinguish it from other British forms. The straight-sided, narrow median sensory field is unique, and none has such markedly zigzag scale-rows, nor completely undivided dorso-lateral and lateral scales.

EXPLANATION OF PLATE 19

Figs. 1–4. *Cephalaspis lyelli* Agassiz. 1, Cephalic shield of lectotype, showing cast of oralo-branchial chamber; for explanation see text-fig. 1. Slightly enlarged. 2, Cast of imperfect counterpart of lectotype, dorsal view. Approximately natural size. B.M. (N.H.) No. P. 3233. 3, The same specimen, side view. 4, Another cast of part of the same specimen showing the enlarged ridge-scale and the spine of the dorsal fin (scale-rows 15–30 approx.). $\times 1\frac{1}{2}$.



WHITE, *Cephalaspis lyelli*

That the form of the scale-rows is not wholly due to distortion is shown by the form of the back of the cephalic shield with which they are parallel, but it is not certain whether the undivided state of the dorsolateral parts of the body-scales is a specific character or the normal condition in the genus, the apparent subdivision of those parts in other species being the result of cracking after death across lines of weakness due to the venous sinuses; but it is clear that they are not regularly formed as restored in *Hemicyclaspis* by Stensiö (1932, text-figs. 15, 23).

From being one of the least-known species of cephalaspid, *Cephalaspis lyelli* is now in many respects as well known as any, but the important result of this study is to show its position in Stensiö's new arrangement of the group, and its identity with *Zenaspis*.

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